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3.3.5 The energy flow through a population of soil *Collembola*

1. INTRODUCTION

It has been suggested (Macfadyen 1963a) that the activities of soil organisms may be responsible for the release and dissipation of up to 75% of the total plant-assimilated energy available to ecosystems. The more general aspects of energy flow through this quantitatively-important community have received attention from Bornebusch (1930), Nielsen (1949, 1961), Cragg (1961), Macfadyen (1963a, 1963b), and Engelmann (1961). Attention has been concentrated on population metabolism, justified by the supposition that in populations of small animals this amounts to a high, constant proportion of total energy flow, perhaps 70—90%; this concept is supported by the results of large-scale surveys such as those of Teal (1957) and Engelmann (1961). Micro-arthropods, especially mites and *Collembola*, are numerically a significant component of the soil fauna, although in terms of biomass and metabolism, relative to nematodes and oligochaetes their rôle may well be small. *Collembola* occur in all soils, at densities between 10,000 and 100,000 per m². Numerous studies of seasonal abundance (and some of life-history) have been made, but since the pioneer work of Bornebusch (1930), no attempt to estimate population metabolism or energy flow has been made.

This paper outlines a study of a population of *Collembola* in *Pteridium* moorland in South Wales, a fuller account of which is being published elsewhere. Four species comprised the bulk of the population, but one species, *Onychiurus*

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procampatus Gisin, constituted about 70% of the total biomass. Work was concentrated on this species which, being of a relatively large size (up to 2 mm) and lacking a furca, had advantages for experimental work. With certain provisos, estimates obtained for this species may be extended to the rest of the population (H e a l e y 1966).

The simultaneous estimation of density, age structure, biomass, growth and population metabolism in any natural population requires complex multivariate analysis. This has not yet been attempted on the data for *O. procampatus* and it is necessary to assess the errors of each estimate separately. This, and other inadequacies in the data, require that this study be regarded only as a preliminary survey.

2. METHODS

The population of *O. procampatus* was sampled with a high-gradient Tullgren extractor (M a c f a d y e n 1961); the efficiency of this apparatus is hard to measure directly but is probably high. The population was sampled according to a stratified random scheme at the end of each month between April 1962 and September 1963, and the resulting sample means were used to calculate the density of the population in each month on a m² basis. Weekly mean soil temperatures were recorded by thermistors and silver voltameter integrators over the period June 1962 to May 1963.

Measurements of the oxygen consumption of *O. procampatus* were made with the Cartesian diver respirometer (H o l t e r 1943). This technique has been widely used by Nielsen and others for work with animals that can be confined in a liquid film. But, as B e r t h e t (1964) has recently shown in a detailed study of Oribatid mites, it may also be successfully used for air-
-breathing arthropods. Due to the great variation in respiratory rate between individuals it is necessary to obtain measurements at different temperatures on the same animal. In his Oribatid study Berthet recorded respiration successively over a range of temperature, keeping the mite in the diver for up to 12 hours. This was not possible with *O. procampatus*, since, even at constant temperatures, the rate of O_2 consumption began to fall after 7 hours, although partial pressure of O_2 fell only 5—6% in this time. *O. procampatus* is probably a continuous feeder (Healey, in litt.), and with a relatively high respiratory rate, it may be that metabolism is quickly affected by lack of food. No solution to this problem has as yet been found and respiration measurements have been made mainly over 3—6 hours.

All weight determinations have been made with a Cann MIO Electrobalance (sensitivity < 2 μg) or a R.I.I.C. EMB-I Electromicrobalance (sensitivity $<$ < 1 μg).

3. RESULTS

3.1 POPULATION DENSITY

The population of *O. procampatus* between June 1962 and May 1963 fluctuated between 2,600 and 13,000, with an annual mean population of 6,000 per m² (Fig. 1). The 95% Confidence Limits for these estimates are wide, with an average of ±35% of the mean (reducing to ±19% when the data is analysed in the appropriate log. transformation). This is consistent with the results of other studies of soil arthropods, and is a consequence of their highly "clumped" distribution; index of aggregation values for *O. procampatus* fall generally between 2.5 and 4.0. The population estimates introduce by far the biggest single source of error in this work.

3.2 BIOMASS

Biomass was estimated by means of a head capsule length/live weight relationship established on 200 animals, to which a regression was fitted on a double log. plot. Individuals weigh 8—12 µg on hatch, females reach 130—180 µg, and males 70 µg. Animals collected in samples were mounted on slides by a standard procedure, sexed, measured and their weight estimated from the regression. The fit of the regression is good, with 95% Confidence Limits for estimates of ±2.5 µg, and error in estimating weight by this method is small. From these weights the biomass of field populations was calculated, by assuming that the size distribution of the population was the same as that of the samples. Over the year biomass varied between 98 and 459 mg, with an annual mean biomass of 217 mg per m² (Fig.1).

3.3 AGE STRUCTURE AND LIFE HISTORY

It has not been possible to find satisfactory morphological criteria for the separation of the instars of *O. procampatus*. H a l e (1965b) finds that six instars may be defined on the basis of head capsule length. In the present study laboratory-bred animals have generally fitted Hale's criteria, but the spread of the measurements of field animals is far too great to permit separation into instars. For the present, the population has been divided into 10 arbitrary weight classes, viz. < 20 µg, 20—30 µg, ... 90—100 µg, > 100 µg. There seems no theoretical objection to this procedure, and since the classes are small compared with broad, variable instar classes, there may be greater accuracy in the calculation of metabolism and production. The representation of these classes in the population between June 1962 and May 1963 is shown in Fig. 2.

The population showed a rather indistinct annual cycle. Newly-hatched

individuals were present at all times, but the major recruitment occured over an extended period from June to October; few adults were present at this time. Between November and April the majority of the population consisted of adults, which showed increasing mortality as the summer recruitment period approached. Over the whole year the average sex ratio was 43 males: 100 females. No males larger than 70 μg were found in the field, whilst females were found up to 180 μg; this difference was also found in culture, where males live only 2—3 months, whilst females live much longer.

3.4 RESPIRATION

A full account of the respiration of *O. procampatus* cannot be given here. A series of measurements of O_2 consumption at 15° C of immature and adult individuals over the whole weight range gave respiratory rates of around 10×10^{-3} μl O_2 per hour for an animal weighing 10 μg, and 32×10^{-3} μl O_2 per hour for an animal weighing 100 μg. The metabolic rate of *O. procampatus* is thus comparable with that of the Nematodes and Enchytraeids studied by N i e l s e n (1961) and is 2—3 times that of Oribatids of similar weight (B e r t h e t 1964). A regression of respiration on live weight was fitted to the data on the conventional double log. plot. The regression coefficient, b, is $0.5029 \pm$ S.E. 0.0854 expresses the rate of increase in metabolic rate with body weight. This value for b is rather low, since as fully discussed by B e r t h e t (1964) the value for small arthropods generally is in the region of 0.7. The fit of the regression is poor, but because rate of increase in metabolism with weight is low, the error in estimating respiration from weight is relatively small (95% Confidence Limits for estimate of O_2 consumption are 2.7×10^{-3} μl O_2 per hour).

Few measurements have been made at temperatures other than 15° C, but those available indicate that the respiration of *O. procampatus* has a high Q_{10} in the region of 3.5—4.0, similar to that found for Oribatids by Berthet. For the present respiration at other temperatures has been estimated by means of Krogh's Curve (K r o g h 1941), which over the field temperature range of 0° C to 16° C has a Q_{10} slightly over 3. As Nielsen has pointed out, the error involved in the use of a standard temperature/respiration curve is small compared with sampling error, and that due to the micro-distribution of field temperature.

3.5 POPULATION METABOLISM

In each month a mean weight for the animals in each size class was calculated and the rate of O_2 consumption estimated from the regression. This value was converted to that for the monthly mean soil temperature by Krogh's Curve. Multiplying by the number of animals in the size class in the field population,

the O_2 consumption of the size class during the month was obtained. Monthly totals of respiration ranged from 10 to 129 ml O_2 per m², giving a total annual population metabolism between June 1962 and May 1963 of 548 ml O_2 per m². The winter of 1962—63 was severe and respiration was greatly depressed, even though biomass was high at this time. Relative to population density and biomass, metabolism was high in the summer months. Of the total annual respiration, 49.6% was due to immature individuals, 38.4% to adult females, and only 12.0% to adult males.

3.6 PRODUCTION

Fig. 2 suggests that no conventional form of cohort analysis for the estimation of mortality and production is possible for *O. procampatus*. Immature individuals amounted to only 17% of the sample of May 1962, compared with 73% in those of June, and the very similar relationship between the samples of April and May 1963 would suggest that a cohort is normally initiated at this time of year. But the recruitment period for this cohort is greatly extended, at least until October, and in these months the age structure of the population becomes complex, permitting no estimate of cohort mortality. Some recruitment also continues in the winter months, as confirmed by laboratory cultures, but whether such late-hatching individuals survive the heavy mortality of adults in April and May is not known.

A provisional estimate of mortality and production has been obtained by summing the estimates of the numbers in each size class for each of the twelve months of the year (Fig. 3). This gives the total recruitment to size class 1 during the year (27,000 individuals), the total representation of size class 2, size class 3, etc. Mortality and production of the cohort may now be estimated from the difference in total numbers in adjacent size classes, using Fig. 3 as a survivorship curve. It is assumed that the mortality fraction between any two size classes reached a mean weight equivalent to the average of the mean weights of the two classes.

Even if Fig. 2 is an accurate representation of the periodic changes in age structure of the population, the use of Fig. 3 as a survivorship curve would be justified only if animals grew straight through all the size classes without interruption. But in fact it is very likely that, especially in the winter, part of the population might remain in a size class over two or more sampling occasions, thereby being counted in that size class more than once, and increasing the apparent mortality from that class. This would mainly affect winter populations whose growth might be slowed by low temperatures, but these consist largely of adults whose contribution to total mortality is relatively small. In any case, the rate of growth of *O. procampatus* is fast, even at 5° C, relative to the width of the size classes (10 μg) and the frequency of sampling, so that the error due to this factor may be quite small.

It is believed that this technique, although no substitute for a proper cohort analysis (should a suitable technique become available), serves to indicate the probable level of production in this species. Production estimated in this way amounted to 994 mg. (Another estimate, for the annual cycle of *O. procampatus*, omits the mature animals of June and July 1963, which belong to the cohort of the previous year, and the juveniles of May 1963, which belong to the following cohort, and amounts to 963 mg). No estimate of production due to cast exuviae is possible, but as these amount to only 2—3% of live body weight, their contribution to production is probably small.

(A minimum estimate of production, which will give some indication whether the above is greatly in excess of true production, may be obtained from the sum of observed increases in population biomass between sampling occasions. This estimate takes no account of biomass increments that occur to some fractions of the cohort at times when their contribution to production is masked by quantitatively greater mortality of biomass elsewhere. Such production, at times of net biomass increment alone, and occurring largely in the summer months and between December and January, amounts to 650 mg).

3.7 EGG MORTALITY

Fecundity in *Collembola* has been fully reviewed by H a l e (1965b). For *O. procampatus*, Hale estimates a fecundity of 9 eggs per female, and using basically the same technique I reach an estimate of 8. Taking the lower figure, and the observed average adult sex ratio of 43 males : 100 females, the average fecundity for the adult population is 5.6 eggs per individual. If the population is in stable equilibrium (and there is no reason to doubt this) each adult is replaced by one adult in the next generation. Thus 4.6 (80%) of the egg output of each individual must die. Therefore the adult population at maximum, i.e. the 7450 individuals found in size classes 3 and 4, represent 20% of the number of eggs originally laid. This amounts to abot 37,000, which accords well with the population survivorship curve. Omitting the juveniles of May 1963, the total population of size class 1 is 24,700 and thus egg mortality amounts to 12,600 or 34%. Eggs weigh 3.9 $\pm$ S.E. 0.2 µg soon after laying and the egg mortality fraction of production thus amounts to 49 mg.

3.8 RESPIRATION OF MORTALITY FRACTION

The estimate of mortality above also permits an estimate of the population metabolism of the individuals that died between sampling dates. This can be obtained by assuming that the animals that died spent an average of two weeks in the population at the annual mean temperature of 8.9° C and had

the average weight at which they died (Tab. I). This assumes that mortality was spread evenly through the year. This is clearly not so, but as most mortality occurred in the summer months, when temperatures were high, the assumption is likely to result in an underestimate. Respiration of these animals amounts to 86 ml, making total population metabolism 548 + 86 ml = 634 ml. No estimate of population metabolism of eggs is possible.

3.9 ASSIMILATION

Some preliminary work has also been done on assimilation in this species. This work is mentioned here mainly to illustrate the procedures involved in assessing energy flow in an animal of this sort, rather than because they are likely to prove correct. *O. procampatus* is very largely a fungal feeder, but from the analysis of gut contents it is not possible to tell which types of soil fungi dominate the diet. Laboratory feeding experiments have been carried out with species of soil fungi (*Mortierella, Ascochyta, Penicillium* and *Mucor*) which are known to be active in decomposition of *Pteridium* (F r a n k l a n d 1966), and are likely to be present in the area where the animal lives. The experiments indicate that at 15° C animals of less than 50 µg weight eat an average dry weight of fungus of 17% of their body weight per day, and animals of 50—100 µg weight about 11%. The amount of the food assimilated varies widely between species of fungi and between different cultures of the same fungus. Estimates of assimilation efficiency, however, all fall within the range 40—70%. This is a high rate of assimilation, but, at least to my knowledge, there are no estimates of assimilation for other fungal feeders available for comparison. It must be remembered that an animal feeding on fungal hyphae receives quantities of highly concentrated fats and carbohydrates. It does not seem wise to take an average rate of assimilation from such data in which the sources of variation are not understood, and I have for the present used 40% as a minimum estimate of assimilation efficiency. Using this figure, it is possible to estimate minimum assimilation in each month of the year, taking account of age structure and temperature (applying the standard temperature — metabolism curve used to correct respiration). These estimates range from 47 mg dry weight of fungal material per m² in January to 575 mg per m² in October, and amount to a total for the year of 2.30 g.

3.10 CALORIFIC EQUIVALENTS

No calorimetric data is available for *O. procampatus* (or for any other *Collembola*), and published equivalents must be used. That used for respiration is the conventional one of 4.8 calories per ml O_2 (S l o b o d k i n 1962), which assumes an R. Q. of 0.82. Published figures for calorific contents of

arthropod tissues fall mainly between 5,000 and 6,500 calories per gram dry weight. Adult *O. procampatus* from the field have a fat content of up to 25% live weight (55% dry weight), and laboratory animals contain even higher percentages of fat. The cuticle amounts to only 2—3% of body weight. It seems reasonable to assume that calorific content is high, and to take 6,000 calories per gram dry weight as a conservative estimate. The dry weight (of adults) is 45% ± S.E. 0.8% of live weight, and the calorific conversion is therefore 2.5 calories per mg live weight. W i e g e r t (1964) obtained 6,300 calories per gram for the calorific value of spittlebug eggs, and in the absence of other information, this equivalent and a dry weight of 45% will be assumed for the eggs of *O. procampatus*. Tab. II sumarises the data on respiration and production and reaches an estimate of annual population energy flow in *O. procampatus* of 5.65 Kcal per m² per annum. Published calorific equivalents for fungal tissue (principally commercial mushrooms) lie around 2,000 calories per gram dry weight: this value applied to 2.30 g of fungal tissue gives an estimate of assimilation by *O. procampatus* of 4.60 Kcal per m² per annum.

4. DISCUSSION

Annual secondary production in *O. procampatus* (1043 mg, 2.61 Kcal per m²) amounts to about 46% total energy flow (5.65 Kcal). As a rough estimate this accords reasonably well with the secondary production [assimilation ratios of 30—40% found in other herbivorous insects by S m a l l e y (1960) and W i e g e r t (1964, 1965)]. But it is in conflict with Macfadyen's suggestion (for instance M a c f a d y e n 1967) that members of the detritus food chain have low production/assimilation ratios, which may in some way be a reflection of the quality of their food, which is material rejected by other trophic levels. Data relevant to Macfadyen's suggestion are rather few, but it is perhaps supported by Engelmann's figure of 18% for the production//assimilation ratio of an Oribatid mite population and by Berthet's (B e r t h e t 1967) similar conclusion. Phillipson's figure (P h i l l i p s o n 1967) of about 30% for *Oniscus asellus* is an intermediate one. There remains the possibility that the high ratio found for *O. procampatus* may be distorted by over-estimation of production. But in fact the minimum estimate of production calculated from net biomass increments alone (Section 3.6) would, when summed with respiration, amount to about 36% of total energy flow. It would appear that the observed production/assimilation ratio is not greatly wrong, and it seems unlikely that more accurate calorimetric data, when it becomes available, will alter the estimate by more than a few percent. The high ratio may reflect the relatively specialized fungal feeding habit of this species, compared with some other soil organisms.

The three independently estimated factors respiration, production and assimilation (of which the latter would seem to be the weakest estimate) may be fitted to the energy flow equation:

$$A = R + P$$
$$5.65 \text{ Kcal} = 3.04 \text{ Kcal} + 2.61 \text{ Kcal}$$

These three estimates use only published calorific equivalents, and the estimate of assimilation is based on the minimum rate of assimilation observed. Even so, the error between the two sides of the equation is only 20%. When calorimetric data becomes available for this species it will be possible to give the equation more precise terms.

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Table I

The calculation of production in *O. procampatus* for the calendar year June 1962 to May 1963

Size class	Numbers	Mean weight μg	Mortality	Mean weight μg	Production mg
1	27,245	13.5	13,710	18.9	249.1
2	13,535	24.2	6,070	29.5	179.1
3	7,445	38.4	—	39.9	—
4	7,455	44.9	3,845	49.8	153.8
5	3,610	54.77	1,010	60.1	60.7
6	2,600	65.4	—	70.2	—
7	3,595	74.9	1,040	80.3	83.5
8	2,555	85.6	775	90.2	69.9
9	1,780	94.5	475	99.3	47.2
10	1,305	104.0	920	110.3	101.5
11	385	116.5	15	120.6	1.8
12	370	124.6	245	127.3	31.2
13	125	130.0	125	130.0	16.3
					994.1 mg

Table II

The calculation of energy flow per m² through the population of *O. procampatus*. June 1962 to May 1963

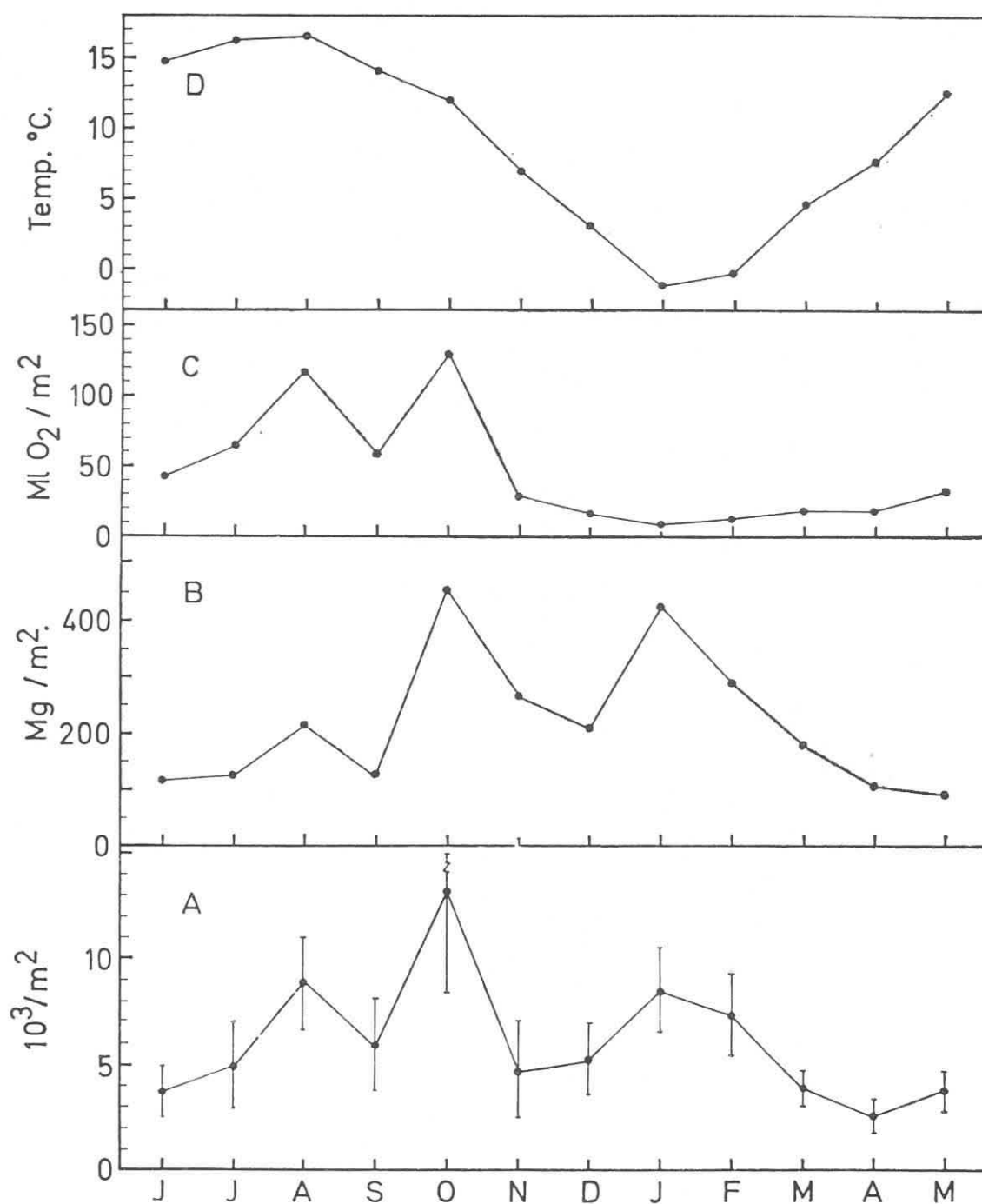|		Calories
Population metabolism	548 ml O_2	2,630
Population metabolism of mortality fraction	86 ml O_2	410
Total		3,040
Production Calendar year	994 mg	2,480
Egg mortality	49 mg	130
Total		2,610
Total energy flow		5,650

Fig. 1. Fluctuations in mean population (A — thousands per m², with 95% Confidence Limits), mean biomass (B — mg per m²) and total population metabolism (C — ml O_2 per m² per month) of *Onychiurus procampatus* between June 1962 and May 1963; D — fluctuation in mothly mean soil temperature
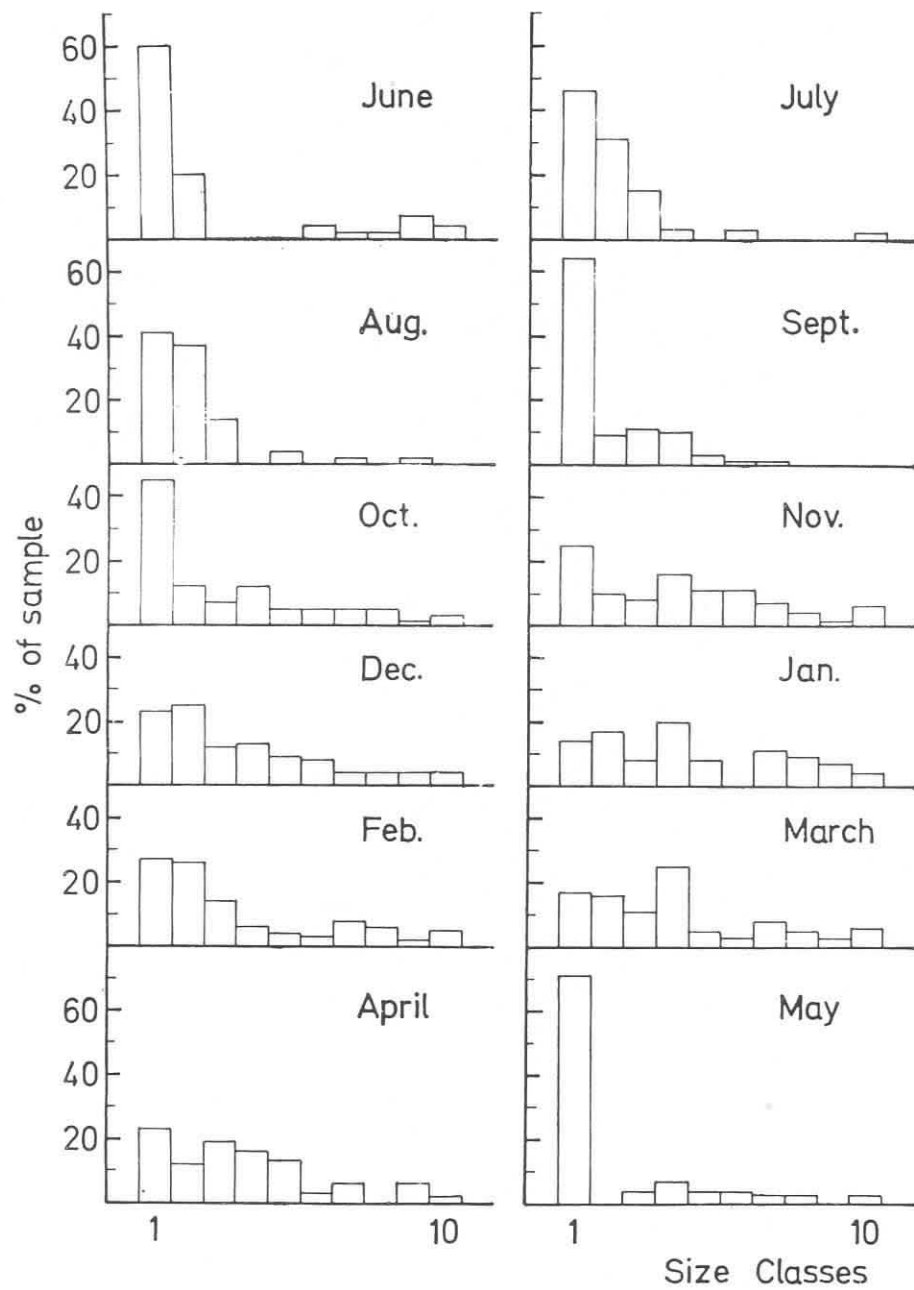
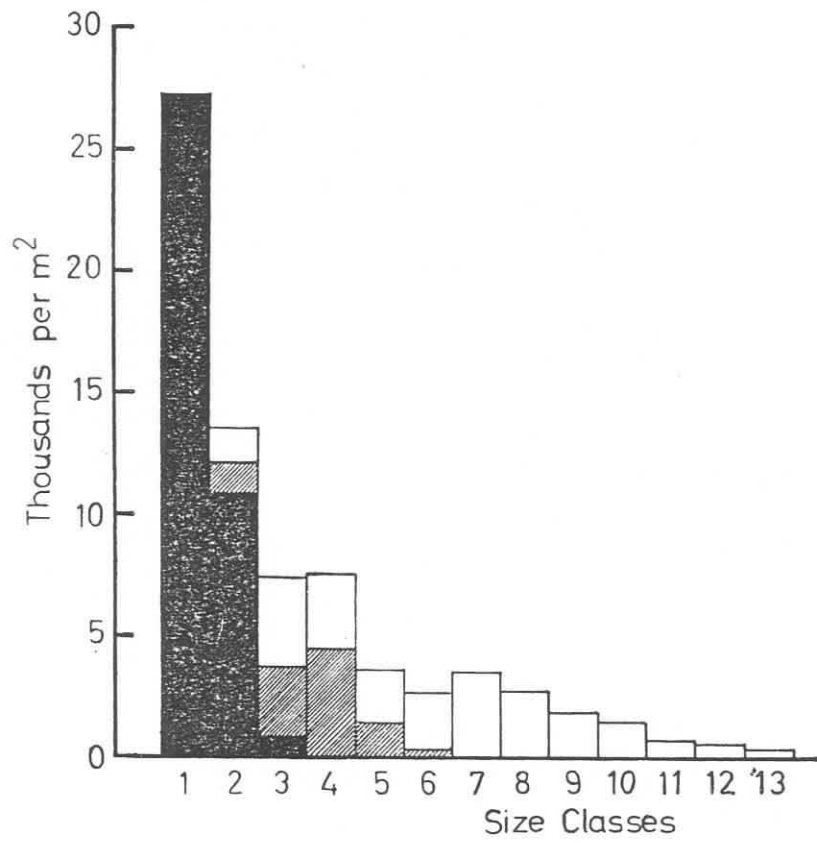Fig. 2. Size class representation in the population of *O. procampatus* between June 1962 and May 1963

Fig. 3. Total number of individuals in each of the size classes in the population of O. *procampatus* in the calendar year June 1962 to May 1963. Immature animals black, males hatched, females blank